Photosynthetic recovery of desiccated intertidal seaweeds after rehydration*

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Abstract Intertidal seaweeds experience periodical desiccation and rehydration to different extents due to the tidal cycles and their vertical distributions. Their photosynthetic recovery process during the rehydration may show different patterns among the seaweeds from different zonations or depths at intertidal zone. In this study 12 species of seaweeds collected from the upper, middle, lower and sublittoral zones were examined. The relationship of the photosynthetic recovery to vertical distribution was assessed by comparing their patterns of photosynthetic and respiratory performances after rehydration following desiccation. Both the photosynthesis and dark respiration declined during emersion, showing certain degrees of recovery after re-immersion into seawater for most species, but the extents were markedly different from one species to the other. The species from upper intertidal zone after being rehydrated for 1 hour, following 2 hours of desiccation, achieved 100% recovery of their initial physiological activity, while most of the lower or sublittoral species did not achieve full recovery. It is the ability to withstand desiccation stress (fast recovery during rehydration), but not that to avoid desiccation (water retaining ability) that determines the distribution of intertidal seaweeds. Such physiological behavior during rehydration after desiccation reflects the adaptive strategy of intertidal seaweeds against desiccation and their capability of primary production in the process of rehydration.

Keywords: seaweeds, desiccation, emersion, intertidal, photosynthetic recovery.

Intertidal seaweeds usually experience hours to days of desiccation during emersion before being immersed again in tide cycles[1]. To some species of seaweeds the desiccation imposed negative effects on photosynthesis and respiration[2—6], it could also enhance the net photosynthesis of most detected seaweeds at the initial phase of the water losing process[5, 7—12]. However, little has been documented on the relationship of photosynthetic recovery with water retaining ability.

Desiccation-resistant performances of intertidal seaweeds were considered to be related to their vertical zonation in the intertidal zone[13—15], while the opposite view considered the reduction of photosynthetic rates to be directly related to thallus water content and not to the habitat they distribute[9, 16]. The ability to maintain active photosynthesis should be correlated with the vertical distribution of intertidal seaweeds. However, how photosynthetic recovery during rehydration after emersion is correlated with the vertical distribution of seaweeds has yet to be investigated[17].

This study investigated the photosynthetic recovery after desiccation in 12 species of seaweeds from different levels of the intertidal zone, aiming to find out the correlation between the ability of recovery and the ability to retain water, and to discuss the relationship between the recovery and their vertical zonations.

1 Material and methods

1.1 Seaweed collection and treatment

Seaweeds were collected from upper, middle, lower and sublittoral zones of the shores at Kannonzaki and Nojima, Kanagawa Prefecture; Banda, Chiba Prefecture and Shimoda, Shizuoka Prefecture, Japan between April 1999 and May 2000. Samples were preserved in an icebox and transported back to the lab within two hours, where they were maintained in aerated seawater at 20 ℃. Experiments were then carried out within 48 hours after the collection.

Twelve species were studied (Table 1), including 2 upper intertidal species, 3 middle intertidal species, 6 lower intertidal species and 1 sublittoral species.

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Table 1. The names, collection areas and vertical distributions of the species used in this study

	Species	Location	Vertical distribution
1	*Porphyra yezoensis*	Nojima, Kanagawa Pref.	Upper littoral
2	*Gloiopeltis furcata*	Banda, Chiba Pref.	
3	*Ishige okamurae*	Shimoda, Shizuoka Pref.	Middle littoral
4	*Myelophycus simplex*	Banda, Chiba Pref.	
5	*Chondracanthus intermedius*	Kannonzaki, Kanagawa Pref.	
6	*Ulva pertusa*	Kannonzaki, Kanagawa Pref.	Lower littoral
7	*Pterocladia capillacea*	Kannonzaki, Kanagawa Pref.	
8	*Sargassum thunbergii*	Shimoda, Shizuoka Pref.	
9	*Chondrus ocellatus*	Kannonzaki, Kanagawa Pref.	
10	*Ahnfeltia paradoxa*	Kannonzaki, Kanagawa Pref.	
11	*Sargassum fusiformis*	Kannonzaki, Kanagawa Pref.	
12	*Gelidium elegans*	Kannonzaki, Kanagawa Pref.	Sublittoral

1.2 Photosynthesis measurements

Net photosynthesis and respiration measurements were conducted in a Plexiglas assimilation chamber maintained in an incubator for temperature control. Photosynthetic and respiration rates under emersed conditions were determined on a basis of the difference in CO_2 concentration between inlet and outlet air by using an infrared gas analyzer (IRGA, Horiba AS-SA-1100). Air was pumped from an air bag at a flow rate of 1.5 L·min^{-1} that had been inflated with outdoor air beforehand. Light was supplied from above the incubator with a lamp (National 500 W), providing 720 μmol/m^2/s of light intensity for photosynthesis measurements. A 10-cm thick water layer was placed between the incubator and the light source to reduce the heat. Light intensity was measured with a light meter (LI-COR LI-250). Dark respiration was determined by completely covering the assimilation chamber with an opaque plastic sheet. The surface temperature of thalli was monitored with a thermometer located in the assimilation chamber.

Photosynthesis (Pn) or dark respiration (Re) rate was calculated by the following equation:

$$Pn \text{ or } Re = \frac{(A - B) \times 273 \times F}{22.4 \times (273 + T) \times W_d}$$

where A and B are CO_2 concentrations (ppm) in air before and after passing through the assimilation chamber respectively; F is the flow rate (L·min^{-1}); T, the surface temperature (℃) of samples; W_d, the dry weight of samples used. As the final results were expressed by molar value, $273/(273 + T)$ was used to convert air volume into the volume under standard condition (0 ℃), where 273 is the absolute temperature of 0 ℃, 22.4 is the coefficient (the volume of 1 mole air under standard condition is 22.4 L).

After the weight was measured, algal samples were put into the assimilation chamber, the Pn and Re were instantly determined as initial values. With the airflow in the system, the water content of the plants was evaporated and gradually reduced. After two hours, the net photosynthesis and dark respiration rates were measured, and the plants were removed out of the assimilation chamber to determine their water content and relative water content.

In the preparatory tests, for some species their photosynthetic rates nearly declined to zero in about 2 hours, while the main purpose of this study is to compare the ability of recovery of different algal species, so a 2-hour of time was chosen to be the desiccation period.

Relative water content (RWC) was calculated with the following equation:

$$RWC = \frac{W_t - W_d}{W_i - W_d}$$

where W_t is the weight determined after 2 hours of desiccation; W_d, the dry weight, which was measured after blotting water drops from the thallus surface with tissue paper and dried 24 hours at 90 ℃ in a drying oven; W_i is the initial fresh weight.

1.3 Recovery measurements

Desiccated plants were re-immersed into seawater of 20 ℃ for their photosynthetic and respiratory recovery. After a period of re-immersion (1 hour), algal samples were taken out for photosynthesis and respiration measurements, in order to assess the recovery. The measurements took about 5 minutes, only caused 1% to 4% of water loss, and this effect on the Pn measurements can be neglected, because Pn did not show detectable change during this extent of

water loss in the preparatory test.

2 Results

Fig. 1 shows the relative water contents (RWC) of the 12 intertidal seaweeds after 2 hours of desiccation at 25 ℃ and 77% relative humidity. Lower intertidal species *Sargassum thunbergii* and *Sargassum fusiforme* retained nearly 80% to 90% of their initial water contents; however, the upper intertidal species *Porphyra yezoensis* had lost most of its water content and only retained 6% of its initial water content, another upper intertidal species *Gloiopeltis furcata* retained 68% of its initial water content.

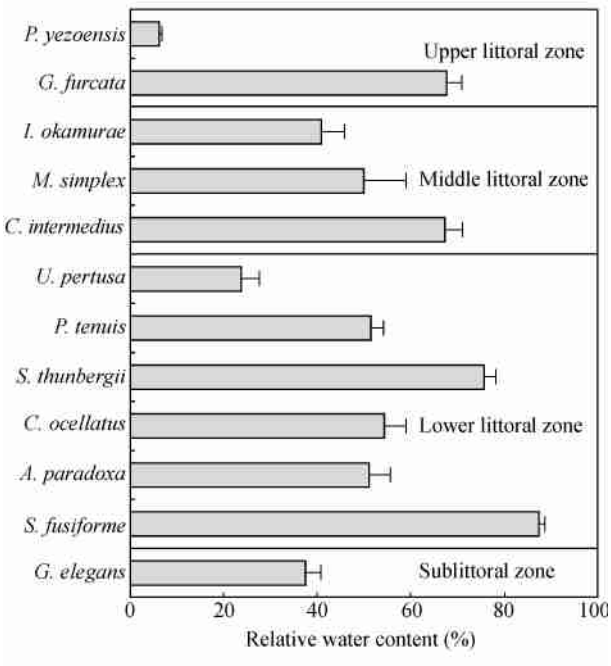

Fig. 1. Remaining of relative water contents of the species after two hours of desiccation at 25 ℃ and 77% relative humidity. Data are the means ±SD of triplicate measurements with more than 10 individuals.

The relationships between the recovery of *Pn* and *Re* and the water loss rate are shown in Fig. 2. Water loss rate was calculated as the average rate during 2 hours of desiccation. Statistical analyses showed that the recovery of *Pn* was positively correlated with the rate of water loss (*Pn*: $n=12$, $r=0.7023$, $P=0.0108$), following a linear correlation pattern, while for *Re* the linear correlation was observed when the 2 completely recovered species (numbers 2 and 9) were omitted (*Re*: $n=10$, $r=0.6736$, $P=0.0327$).

The relationship between the ability of recovery and the vertical distribution of the 12 species is shown

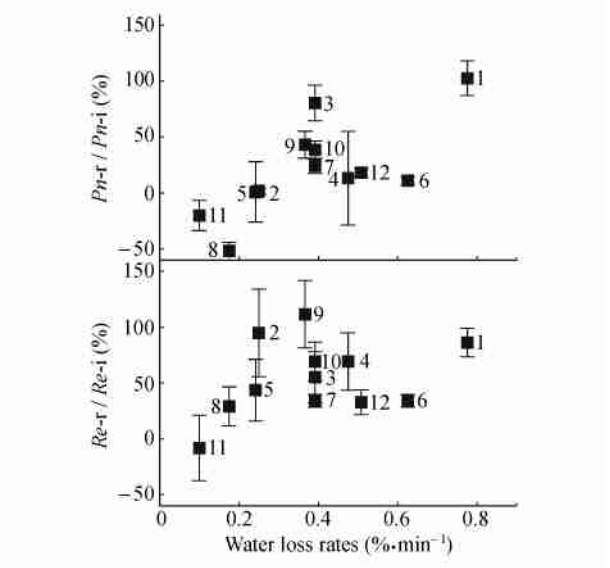

Fig. 2. The relationships between the changes of net photosynthesis (*Pn*) and dark respiration (*Re*) and the rate of water loss in the 12 species. The tests were performed on the seaweeds rewetted in seawater after two hours of desiccation. *Pn*-i and *Re*-i are the photosynthesis and respiration rates measured before desiccation started (initial values). *Pn*-r and *Re*-r are the photosynthesis and respiration rates measured after desiccation and being re-immersed into seawater.

in Fig. 3. After an hour of re-immersion into seawater, all of the species in upper and middle intertidal zones that had their *Pn* dropped during emersion recovered to their initial values, regardless the extents of the decline after two hours of desiccation (numbers 1 and 3 in Fig. 3). While for the lower or sublittoral species, the recoveries are detectable, but not complete compared with their higher intertidal counterparts (numbers 6, 9, 10 and 12 in Fig. 3).

3 Discussion

The studied species showed different abilities to retain water content. However, no correlation was found between the ability to retain water content and their vertical distribution in the intertidal zone. The upper intertidal species, *Porphyra yezoensis*, lost water faster than the lower intertidal form, *Sargassum fusiforme*. Therefore, the ability to retain water content is very crucial for the survival of upper intertidal species during severely desiccating period. Such ability must be related not only to the physiological but also to morphological features of the seaweeds, i.e. sheet-like species loses water faster than the tube-like species. The surface to volume ratio of a thallus may also affect the performance of the water retaining ability, as this ability is closely correlated with the evaporating surface area [18] as reported by previous re-

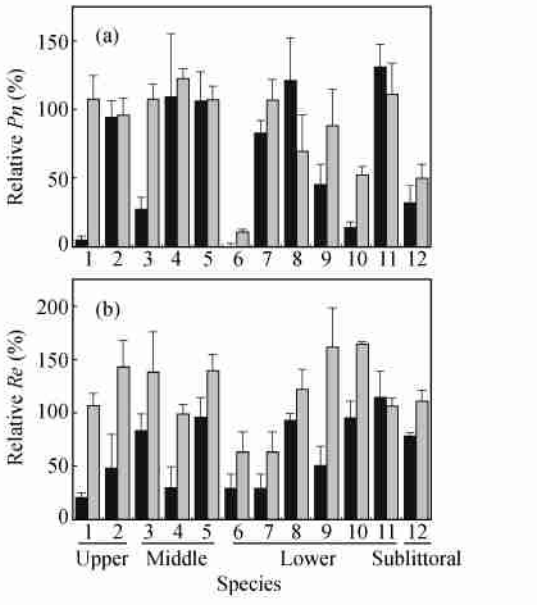

Fig. 3. Net photosynthesis (a) and dark respiration (b) relative to their controls (initial values). The numbers are corresponding to the species in Table 1. Data are the means ±SD of triplicate measurements with more than 10 individuals. The black bars show the relative *Pn* or *Re* (calculated by the ratios between the values of *Pn* or *Re* of thalli after 2 hours of desiccation and the values that desiccation has not advanced) of desiccated thalli; the gray bars show the relative *Pn* or *Re* (calculated by the ratios between the values of *Pn* or *Re* after 1 hour of re-immersion into seawater, following 2 hours of desiccation, and the values of *Pn* or *Re* that were measured before desiccation advanced) of re-immersed thalli. The numbers are corresponding to the species in Table 1. Data are the means ±SD of triplicate measurements with more than 10 individuals.

search.

Previous studies have reported on the recovery of photosynthesis after desiccation[8, 10, 11]. Seaweeds are capable of getting their photosynthesis recovered completely, as long as desiccation did not exceed a certain level[1, 9]. The *Pn* of *Porphyra linearis* recovered quickly after the desiccated thalli were rehydrated, showing the ability to achieve full recovery[10]. In the present study, the extents of recovery are evidently related to the rate of water loss, the extent of recovery calculated by the difference of photosynthesis and respiration activities between the desiccated samples and the re-immersed ones are positively correlated with the rate of water loss (Fig. 2). The species that have higher rate of water loss usually have more obvious recovery, while the species with higher water retaining ability do not get their physiological activities boosted clearly after re-immersion. These results demonstrated that species distributed at upper parts of the intertidal zone have adapted to recycling of desiccation and rehydration according to the tidal cycles. For the lower intertidal species, *Sargassum thunbergii* (number 8) and *Sargassum fusiforme* (number 11) showed a declined photosynthesis while being rehydrated (Fig. 3). This indicates that the desiccation treatment results in damage to their photosynthetic apparatus, and that they were not adapted to the environmental stress as compared to the high intertidal counterparts.

In the present investigation, there were obvious differences between species in their ability of recovering photosynthetic activities after desiccation. Furthermore, based on the results of the mean values of the photosynthetic recovery of the 12 species (Fig. 3), it is obvious that the differences in recovery ability are related to their vertical distribution in the intertidal zone. Based on the data obtained, it is reasonable to come to the conclusion that it is the ability to withstand desiccation stress (fast recovery during rehydration), but not that to avoid desiccation (water retaining ability) that determines the distribution of intertidal seaweeds. It is also evident that seaweeds growing in the intertidal zone perform active photosynthesis during the period of rehydration, and the recovery process contributes to the primary production in coastal waters where seaweeds are abundant.

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